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Perceiving Social Interactions in the Posterior Superior Temporal Sulcus

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Abstract

Primates are highly attuned not just to social characteristics of individual agents, but to social interactions between multiple agents. Here we report a neural correlate of the representation of social interactions in the human brain. Specifically, we observe a strong univariate response in the posterior superior temporal sulcus (pSTS) to stimuli depicting social interactions between two agents, compared to a) pairs of agents not interacting with each other, b) physical interactions between inanimate objects, and c) individual animate agents pursuing goals and interacting with inanimate objects. We further show that this region contains information about the nature of the social interaction, specifically whether one agent is helping versus hindering the other. This sensitivity to social interactions is strongest in a particular subregion of the pSTS but extends to a lesser extent into nearby regions previously implicated in theory of mind and dynamic face perception. This sensitivity to the presence and nature of social interactions is not easily explainable in terms of low-level visual features, attention, or the animacy, actions, or goals of individual agents. This region may underlie our ability to understand the structure of our social world and navigate within it.

Significance Statement

Humans spend a large percent of their time perceiving the appearance, actions, and intentions of others, and extensive prior research has identified multiple brain regions engaged in these functions. But social life depends on the ability to understand not just individuals, but groups and their interactions. Here we show that a particular region of the posterior superior temporal sulcus responds strongly and selectively when viewing social interactions between two other agents. This region further contains information about whether the interaction is positive (helping) or negative (hindering), and may underlie our ability to perceive, understand, and navigate within our social world.

Introduction

Humans perceive their world in rich social detail. We see not just agents and objects, but agents *interacting with each other*. The ability to perceive and understand social interactions arises early in development (1) and is shared with other primates (2–4). Although considerable evidence has implicated particular brain regions in perceiving the characteristics of individual agents—including their age, sex, emotions, actions, thoughts, and direction of attention – it is unknown whether specific regions in the human brain are systematically engaged in the perception of third-party social interactions. Here we provide just such evidence for sensitivity to the presence and nature of social interactions in the posterior superior temporal sulcus (pSTS).

To test for the existence of a brain region preferentially engaged in perceiving social interactions we identified five neural signatures that would be expected of such a region. First, the region in question should respond more to stimuli depicting multiple agents interacting with each other than multiple agents acting independently. Second, this response should occur even for minimalist stimuli stripped of the many confounding features that co-vary with social interactions in naturalistic stimuli. Third, the response to social interactions should not be restricted to a single set of stimulus contrasts, but should generalize across stimulus formats and tasks. Fourth, the presence of a social interaction should be unconfounded from the presence of an agent's animacy or goals. Fifth, the region in question should not merely respond more strongly to the presence of social interactions, but should also contain information about the nature of those interactions. To test for these five signatures, we scanned subjects while they viewed two different stimulus sets that reduce social interactions to their minimal features: two agents, who are acting with temporal and semantic contingency.

Prior studies have reported neural activations during viewing of social interactions (e.g. (5, 6), see also (7) for a review of related studies), but did not provide evidence for the selectivity of this response. Two other studies (8, 9) found activations in numerous brain regions when people viewed social interactions between two humans, versus two humans engaged in independent activities, both depicted with point-light stimuli. However, in both studies the task was to detect social interactions, so the interaction condition was confounded with target detection, rendering the results hard to interpret. Many other fMRI studies have shown activations in and around the pSTS when subjects view social interactions depicted in shape animations (10–16) based on the classic stimuli of Heider & Simmel (17). But these prior studies have generally interpreted the resulting activations in terms of the perception of animacy or goal-directed actions, or simply in terms of their general "social" nature, without considering the possibility that they are specifically engaged in the perception of third-party social interactions.

Notably, a recent study in macaques found regions of frontal and parietal cortex

that responded exclusively to movies of monkey social interactions, and not to movies of monkeys conducting independent actions, or interactions between inanimate objects (4). If humans have a similarly selective cortical response to social interactions, where might it be found in the brain? One region that seems a likely suspect for such a response is the posterior superior temporal sulcus (pSTS), which has been previously shown to respond during the perception of a wide variety of socially significant stimuli including biological motion (18), dynamic faces (19), direction of gaze (20), emotional expressions (21), goal-directed actions (22), and communicative intent (23).

To test for a cortical region sensitive to the presence of social interactions, fitting some or all of the five criteria outlined above, we first contrasted responses to point-light displays of two individuals who were interacting with each other versus acting independently. We replicated prior unpublished findings from our lab that most subjects show a preferential response in the pSTS to social interactions in this contrast (24). We then asked if this response generalizes to social interactions depicted using very different stimuli: shape animations. To unconfound responses to social interactions in the shape stimuli from responses to merely animate agents, or the goal-directed actions of those agents, we included a contrasting condition in which a lone animate agent pursues individual goals (25, 26). Finally, we tested whether the region showing a preferential response to social interactions contains information about the nature of that social interaction (helping versus hindering). We find sensitivity to the presence and nature of social interactions in a region of the pSTS that cannot be explained by sensitivity to physical interactions or to the animacy or goals of individual agents.

Results

Experiment 1

A region in the pSTS is sensitive to the presence of social interactions

To identify brain regions sensitive to the presence of social interactions, we scanned fourteen participants while they viewed video clips of point-light walker dyads engaged either in a social interaction or in two independent actions (Figure 1a). We used three of four runs from each subject to perform a whole-brain group random effects analysis. This group analysis revealed a region in the right posterior STS (MNI coordinates of voxel with peak significance: [54, -43, 18]) that responded significantly more to social interactions than independent actions (Figure 2a). Apart from a weaker spread of this activation more anteriorly down the right STS and weaker activity in superior medial parietal regions bilaterally (see Supplemental Figure 1), no other cortical region reached significance in this contrast.

The random effects group analysis showed that a preferential response to social interactions is significant and anatomically consistent across subjects. However, group analyses are not ideal for characterizing the functional response of the

region, because most functional regions do not align perfectly across subjects so the responses of specific regions are usually blurred with those of their cortical neighbors (27). To more precisely characterize the functional response of the region we therefore defined functional regions of interest (fROIs) in each subject individually. To do this, we selected the top 10% of interaction-selective voxels (i.e. the voxels with the lowest p values in the contrast of interacting versus independent point-light conditions) for each subject within the region identified by the group analysis, using the same three runs of data as in the above group analysis. This individually-defined fROI will be referred to here as the "Social Interaction functional Region of Interest", or "SI-fROI". As in other previous group-constrained subject-specific analyses (28, 29), this method is an algorithmic way to select individual subject fROIs without subjective judgement calls, while allowing for individual variation between subjects' fROI locations, yet still broadly constraining them to the region defined by the group analysis.

We quantified the response to social interaction in each subjects' fROI using the held out run from the point-light experiment, and found a significantly higher response to social interactions over independent actions ($p = 9.5x10^{-5}$, paired t-test, Figure 3a). Twelve out of 14 participants showed the presence of this SI-fROI, as defined with a threshold of $p<0.005$. All 14 subjects showed a greater response to interacting versus independent videos in held out data in the top 10% of voxels, indicating this sensitivity was present in all subjects. In addition, six of fourteen subjects showed a significantly greater ($p<0.005$) response to socially interacting versus independent point-light displays in the left hemisphere near the pSTS. Because this region was not found consistently across subjects, and did not reach significance in the group analysis, we did not analyze it further.

Relationship to nearby regions of interest

We next asked how the SI-fROI compares in location and response profile to established nearby regions engaged in other social tasks, namely the right TPJ (30, 31) and the right pSTS "face" region (which will be referred to henceforth in this paper as the pSTS face region, because that is the contrast by which it is defined, even though this region is now known to respond similarly to voices (32–34)). To define these fROIs, we ran standard face (35) and theory of mind localizers (36) and used a similar group-constrained subject-specific method as described above. We again selected each individual subject's top 10% of voxels for the relevant contrast within a group map defined based on a large number of subjects in prior studies (29, 37). We also identified motion-sensitive region MT using the top 10% of voxels that responded more to moving shapes than static task instructions in Experiment 2 (see below) within the Freesurfer anatomical MT parcel, see Methods.

These fROIs showed a systematic spatial organization across subjects (Figure 2b, Supplemental Figure 2), with the SI-fROI generally residing anterior to the TPJ and superior to the pSTS face region. The SI-fROI showed some overlap with these other fROIs in individual subjects. The overlap between the SI-fROI

and the TPJ constituted on average 8% of the SI-fROI (the number of overlapping voxels divided by the number of voxels in the SI-fROI) and on average 2% of the TPJ. The overlap with the face STS region was on average 1% of the size of the SI-fROI and 1% of the size of the the pSTS face region (see Supplemental Table 1). To examine the extent to which these regions represent distinct information, we removed these few overlapping voxels between the SI-fROI and the other fROIs in subsequent analyses.

The pSTS face region responded significantly more to social interactions than independent actions ($p = 0.014$), but this contrast was not significant in either the TPJ or MT ($p = 0.21$ and 0.56, respectively). Further, a two-way ANOVA, with fROI (SI-fROI versus TPJ versus pSTS-face versus MT) and the social interaction contrast (point-lights interacting vs. independent) as repeated-measures factors, revealed a significant interaction ($F(3,13) = 10.16$, $\eta_p^2 = 0.43$, $p = 4.5 \times 10^{-5}$). This two-way interaction reflected significantly greater sensitivity to social interactions in the SI-fROI than each of the other fROIs ($F(1,13) = 17.02$, $\eta_p^2 = 0.57$, $p = 0.0012$; $F(1,13) = 16.14$, $\eta_p^2 = 0.55$, $p = 0.0015$; $F(1,13) = 23.13$, $\eta_p^2 = 0.64$, $p = 0.00034$, for TPJ, pSTS-face, and MT respectively).

Sensitivity to other social dimensions

The analyses above indicate that the SI-fROI is significantly more selective for social interactions than each of the three nearby regions, pSTS-face, TPJ, and MT, and the pSTS face region is the only other fROI that shows a significant effect in this contrast. Does the SI-fROI differ from these nearby fROIs in other aspects of its response profile? First, we find that the SI-fROI shows a small but significant response to the theory of mind contrast (false belief > false photo, $p = 0.0042$) and face contrast (faces > objects, $p = 0.01$). On the other hand, the SI-fROI is significantly less sensitive to these contrasts than its cortical neighbors, as demonstrated by a significant interaction of i) SI-fROI versus TPJ x false belief versus false photo ($F(1,13) = 22.93$, $\eta_p^2 = 0.64$, $p = 0.00035$) and ii) SI-fROI versus pSTS-face x faces versus objects ($F(1,13) = 6.95$, $\eta_p^2 = 0.35$, $p = 0.021$). Overall, these results indicate that while the social interaction region is both spatially close to and shares some functional information with the TPJ and pSTS face regions, its functional response profile differs significantly from each of these regions.

Experiment 2

To investigate the nature of the social interaction information represented in the SI-fROI, we scanned the same subjects while they viewed 12s videos of animations containing moving shapes from four different conditions: help, hinder, physical interactions, and animate (Figure 1b, Supplemental Videos 1-4). The help and hinder videos consisted of two shapes engaged in a social interaction, and could be divided into two segments. During the first approximately six seconds, one shape moved in a clearly goal-directed fashion. The other shape was either stationary or moved very little during this period, but in the context of

the experiment the percept of a social interaction was nonetheless clear during this period, with the second shape apparently "watching" the first shape. During the second six seconds of each video, the first shape was either helped or hindered in its goal by the second shape. We modeled each of these six second periods separately in a GLM analysis. The first six seconds of these videos were better controlled for motion and designed to provide a clean contrast between the interacting (help and hinder) and non-interacting (animate and physical interaction) conditions, while the second six seconds were designed to most vividly depict helping and hindering. The two interaction conditions (help and hinder) were contrasted with the physical interaction videos, which consisted of two shapes moving in an inanimate fashion, like billiard balls colliding with each other and their background. Finally, to measure the extent to which activity in the SI-fROI is driven by animacy and goals of individuals, in the absence of social interactions, the fourth set of "animate" videos consisted of a single goal-driven shape (five videos used the shape trajectory from shape 1 from a random half of the help videos, and five videos used the shape trajectory from the half of the hinder videos whose help video trajectories were unused). Two subjects (S1, S2) saw a different version of the "animate" videos and are not included in the following analysis, but are included in the final help versus hinder analyses.

Social interaction sensitivity generalizes to shape stimuli

To test whether this new set of stimuli elicited social interaction responses in the pSTS, we compared the responses to the help and hinder videos (social interaction) to the physical interaction videos in our four fROIs. For this contrast, we used the responses to the first six seconds of the shape videos, which were better controlled for low-level motion across the different conditions than the second six seconds. Although the second shape moved little or not at all during this initial period of each video, the percept of a social interaction was nonetheless clear during this period, an impression validated with ratings of naïve viewers on Mechanical Turk (see Supplemental Figure 5C). The SI-fROI showed a significantly greater response to this first 6 seconds of the interaction videos (help and hinder) than physical interactions ($p = 1.3 \times 10^{-4}$, paired t-test between the average of help and hinder and the physical interaction condition). The STS-face region also showed a significantly greater response to socially interacting shapes ($p = 2.9 \times 10^{-4}$). The TPJ showed a trend toward a higher response to the social interaction, but it did not reach significance ($p = 0.056$), and MT did not show a significant difference ($p = 0.67$).

A two-way ANOVA, with ROI (SI-fROI versus TPJ versus pSTS-face versus MT) and social vs. physical interaction videos as repeated-measures factors, revealed a significant interaction ($F(3,11) = 8.03$, $\eta_p^2 = 0.42$, $p = 3.7 \times 10^{-4}$). This two-way interaction reflected significantly greater sensitivity to social interactions over physical interactions in the SI-fROI than the TPJ and MT ($F(1,11) = 27.5$, $\eta_p^2 = 0.71$, $p = 2.75 \times 10^{-4}$; and $F(1,11) = 13.17$, $\eta_p^2 = 0.55$, $p = 0.004$, for TPJ, pSTS-face, respectively), but not the STS-face region ($F(1,11) = 2.7$, $\eta_p^2 = 0.20$, p =

0.13). These results generalize the sensitivity of the SI-fROI to social interactions found Experiment 1 to a new and very different stimulus set.

Sensitivity to animacy and goals

We have argued that the SI-fROI is specifically sensitive to the interaction of two shape stimuli. But is this region also driven by the animacy or goals individual agents? To find out, we measured the response of the SI-fROI to the single animated shape videos, where the shapes were both animate and goal driven, and contrasted this with the physical interaction condition, where shapes were neither animate nor goal-driven, over the first 6 seconds of each video. Twenty independent raters on Mechanical Turk rated this segment of the video to be significantly more animate (mean rating 3.14/4) and goal-directed (mean rating 3.22/4) than the physical interaction condition (mean rating 2.0/4 for animacy and 1.6/4 for goal-directed, $p = 5.4 \times 10^{-7}$ and 8.5×10^{-11}, respectively). The SI-fROI showed no difference in response to the animate versus physical interaction conditions ($p = 0.44$, paired t-test). Similarly, the TPJ did not show a higher response to animate versus physical videos ($p = 0.15$), and MT showed a higher response to physical than animate videos ($p = 0.018$). However, the STS-face region did show a significantly greater response to animate than physical interaction conditions ($p = 0.002$). In the second 6s of the shape movies, the SI-fROI did show a slightly higher response to the animate condition than the physics condition (Supplemental Figure 3), perhaps indicating a response to success or failure in attaining goals. The lack of such an effect in the first six seconds, when the goals and animacy of the shapes in the animate videos were very clear (Supplemental Figure 5) indicates that the presence of animacy and individual goals on their own are not sufficient to activate this region.

A whole-brain group random effects analysis showed a region in the posterior STS that responds significantly more to the animate than physical videos (Supplemental Figure 4). This activation is anterior to the highly significant region observed for the social interaction contrast (Figure 2a). This group analysis, combined with the lack of response to the animate video conditions in the SI-fROI, suggests that separate regions in the pSTS process social interactions versus animacy and goal-directed actions.

Representation of helping and hindering

The analyses above reveal a clear univariate sensitivity to presence of social interactions in the SI-fROI in the pSTS. Does this region also contain information about the nature of that social interaction? To answer this question, we used multi-variate pattern analysis (MVPA) to decode whether the video depicted a helping or hindering interaction (1). We used the beta values for each voxel from second six seconds of each of the ten help and hinder movies (when the helping or hindering action occurs) as input features to a linear support vector machine (SVM) classifier. We trained this classifier on data from nine pairs of matched help and hinder videos (i.e. two videos that begin very similarly, but end with a helping action or a hindering action), and tested it on data from tenth held out

pair of help/hinder videos. We repeated this analysis for each held out video pair. This analysis provides a strong test of generalization across our different stimulus pairs, because the objects on screen and location and movement patterns of the shapes are more similar within a matched help/hinder pair than they are across different help videos, or across different hinder videos.

We can robustly decode helping versus hindering in the SI-fROI ($p = 1.2x10^{-4}$) and TPJ ($p = 5.0x10^{-4}$) and to a lesser extent in the STS-face region ($p = 0.0086$). Importantly, we cannot decode help vs. hinder in MT ($p = 0.39$; we also do not observe a univariate difference between the second six seconds of help and hinder in the univariate MT response, see Supplemental Figure 3).

Discussion

We report here a region of the pSTS, detectable in most subjects individually, that responds about twice as strongly when viewing simple point-light videos of two people interacting compared to two people acting independently. This selective response to social interactions is unlikely to result from differences in attentional engagement or low-level differences in the stimuli, because it is not found in visual motion region MT which is sensitive to both (38). Neither can the response to social interactions be reduced to a response to the animacy, actions, or goals of individual actors, as these attributes alone did not drive this region more than inanimate shapes. Further, the strong sensitivity to social interactions depicted in point-light displays in Experiment 1 generalizes to the very different depictions of social interactions in animated shapes in Experiment 2. Finally, the same region contains information about the nature of the social interaction, specifically whether it is positive (helping) or negative (hindering). Taken together, this region exhibits all five signatures we predicted for a region selectively engaged in perceiving social interactions.

The present findings are further strengthened by the fact that an independent study with different stimuli and subjects yielded highly similar results, including a preferential response to social interactions compared to independent actions that generalizes from point-light displays to shape animations, and the ability to decode cooperative versus competitive social interactions from the same region (39).

The selective response to social interactions reported here does not appear to take the form of a discrete cortical region with sharp edges that is exclusively engaged in perceiving social interactions. Though the peak activation to social interactions is largely non-overlapping with the TPJ (as suggested by prior work (15)) it shows a significantly higher response to false beliefs than false photos (the standard theory of mind localizer contrast). This region also shows a significantly higher response to faces than objects. On the other hand, responses are overall much lower in all of these conditions than they are for social interactions, and some of the response to theory of mind stories and faces may

be due to the social interactions implied by these stimuli. The sensitivity to social interactions also spills over into the nearby TPJ and pSTS face region, albeit in weaker form. Thus, the sensitivity to social interactions reported here may be better thought of as not a discrete module but a peak in the landscape of partially overlapping sensitivities to multiple dimensions of social information in the STS.

The sensitivity to social interactions reported here may further inform our understanding of previously reported cortical responses to social stimuli. The pSTS "face" region has remained an intriguing mystery ever since it was shown to respond three times as strongly to dynamic as static faces (35), and to respond equally to videos of faces and recordings of voices (32, 34, 40). Here we find that this region also shows some sensitivity to both the presence and nature of social interactions depicted with point-light displays and animated shapes, implicating this region in the perception of third-party social interactions. One possibility is that the strong response of this region to dynamic face stimuli may be due to the fact that most of the faces in our study are clearly interacting with a third person off screen. This hypothesis predicts a higher response in this region to dynamic faces interacting with off-screen third-party agents than dynamic faces engaged in individual non-interactive activities.

A number of prior studies that reported activations in the pSTS during viewing of animations of interacting shapes (10, 13, 14, 16, 41, 42) have interpreted these activations as reflecting inferences about the intentions or animacy of individual actors. Our data suggests that these activations cannot be primarily driven by either the animacy or goals of these shapes, but instead likely reflect the perception of social interactions. Importantly, though, many other studies have found sensitivity in nearby regions to the intentions of individuals that cannot be straightforwardly accounted for in terms of a social interaction (Vander Wyk et al. 2009; Wheatley et al, 2007), and we also observed portions of the STS that responded to individual agents pursuing goals (Supplemental Figure 4). Thus, the currently available evidence suggests the existence of at least four dissociable responses in this general region: the TPJ, specialized for inferring the thoughts of others, the pSTS-"face" region, another STS region responsive to the agency and/or goal-directed actions of individual actors, and the selective response to social interactions reported here (see also (15)).

Why might the analysis of social interactions between third-party agents be important enough that a patch of cortex is allocated to this task? Clearly, humans care a great deal about social interactions, and recognizing the content and valence of others' interactions plays several important roles in our daily lives. First, social interactions reveal information about individuals; we determine whether a person is nice or not by how that person treats others. Social interactions also improve the recognition of individual agents and their actions (44). In addition, social interactions reveal the structure of our social world: who is a friend (or foe) of whom, who belongs to which social group, and who has power over whom. Understanding these social relationships is crucial for

deciding how to behave in the social world, and in particular for deciding whether and when to trade off our individual self-interest for the potential benefits of group cooperation (45). To inform such complex decisions, the perception of social interactions likely interacts with other relevant social dimensions such as the gaze direction, emotions, thoughts and goals of others, perhaps providing a clue about why these functions reside nearby in cortical space.

Humans are not the only animals with a strong interest in third-party social interactions, and recent work shows regions in macaque cortex that respond exclusively during viewing of such interactions (4). However, the regions selectively responsive to social interactions in macaques are situated in the frontal and parietal lobes, not temporal lobe, and are therefore unlikely to be strictly homologous to the region described here. Macaques do show a sensitivity to social interactions in the lateral temporal lobe, but that region responds similarly to interactions between inanimate objects, in sharp contrast to the region reported here in humans. Nonetheless, it is notable that the perception of social interactions is apparently important enough in both humans and macaques that a region of cortex is allocated largely or exclusively to this function, even if those regions are not strict homologues.

This initial report leaves open many questions for future research. First, as usual with fMRI alone, we do not yet have evidence that this region is causally engaged in the perception of social interactions. In particular, while MVPA presents a powerful tool to read out neural patterns, such as those distinguishing helping versus hindering, the fact that scientists can read a certain kind of information out of a given region does not necessarily mean that the rest of the brain is reading that information out of that region (46). Future studies might investigate this question with TMS or studies of patients with brain damage. Second, it is unknown when or how the selective response to social interactions develops, and whether its development requires experience viewing social interactions. Behaviorally, human infants are highly attuned to social interactions, and distinguish between helping and hindering by 6 months of age (1), perhaps suggesting that this region may be present by that age. Third, the structural connectivity of this region and its interactions with the rest of the brain are unknown. Beyond the obvious hypothesis that this region is likely connected to other parts of the social cognition network, it may also be connected with brain regions implicated in intuitive physics (47), since the distinction between helping versus hindering hinges fundamentally on understanding the physics of the situation.

Finally, and most importantly, we have barely begun the to characterize the function of this region and the scope of stimuli it responds to. Will it respond to a large group of people interacting with each other, as in a cocktail party, football game, or lecture hall? It is further unknown what exactly this region represents about social interactions (The mutual perceptual access of two agents? Social dominance relations between two people? The temporal contingency of actions?

All of the above?) and whether these representations are calculated directly from bottom up cues or from top-down information about goals and social judgements (48). More fundamentally, is this region a unimodal visual region or will it respond to other types of stimuli, such as an audio description or verbal recording of an interaction? This region's functional dissociation from low-level visual motion region MT, and proximity to other regions integrating multimodal social information in the STS, lead to the intriguing possibility that it responds to abstract, multimodal representations of social interactions. Although considerable further work will be required to precisely characterize the representations and computations conducted in this region, the initial data reported here suggest this work is likely to prove fruitful.

Methods

Participants

Fourteen subjects (ages 20-32, 10 female) participated in this study. All subjects had normal or corrected to normal vision and provided informed written consent before the experiment. The MIT Committee on the Use of Humans as Experiment Subjects approved the experimental protocol.

Paradigm

Each participant performed four experiments over the course of 1-3 scan sessions. The first experiment consisted of point-light dyads that were either engaged in a social interaction (stimuli from (49)) or performing two independent actions (stimuli from (50)). Individual videos ranged from three to eight seconds and there were three videos presented in each 16s block. Each run consisted of eight blocks of each condition and two 16s fixation blocks presented at the middle and end of each run for a total time of 160 s per run. Stimulus conditions were presented in a palindromic order. This experiment was split over the course of two runs, and was repeated twice for a total of four runs. Subjects passively viewed these videos.

In the second experiment subjects viewed 12s videos of one or two simple shapes moving in one of four conditions: help, hinder, animate, or physics. In the first three conditions the shapes were portrayed as animate and one shape in each video had a goal (e.g. the blue square wants to climb a hill, see Figure 1). In the help and hinder conditions, a second shape was present, and the second shape either helped (e.g. pushed the first shape up the hill) or hindered (e.g. blocked the first shape from the top of the hill) the first shape achieve its goal. In the third “animate” condition, the first shape’s motion was kept the same as in the help or hinder videos but the second shape was removed so there was only one shape on the screen achieving or failing at its goal (half of the videos were shape 1 from help videos and the half of the videos were shape 1 from the hinder videos). In all three conditions, the first shape’s goal was kept constant across each set of three videos (help, hinder, and animate) and the 12s videos consisted of two parts: the first 6s where one shape establishes a goal, and the second 6s where that shape is either helped or hindered, or does or does not achieve its goal alone (in the “animate” condition). In a fourth “physics” condition, the shapes were depicted as inanimate billiard balls moving around the same scene as the first three videos and having physical collisions with each other and the background. The videos with two shapes contained a red and blue shape (color counter balanced in help/hinder videos between shape 1 and shape 2), the animate videos contained one blue shape. After each video subjects were given four seconds to answer the question, “How much do you like the blue shape” on a scale of 1-4 (the response order flipped halfway between each run to avoid motor confounds). Subjects viewed ten different sets of matched videos for each of the four conditions, for a total of 40 different videos presented over two runs. Each run lasted 320 seconds (20 videos x (12 second video + 4 second

response period)). Participants saw each video a total of four times, over eight total runs.

Finally, we performed two localizer experiments to identify nearby regions in the pSTS also known to process socially relevant stimuli: the STS “face” region (in quotes because it responds equally to voices) and the theory-of-mind selective region in the temporal parietal junction (TPJ). To localize the “face” region, subjects viewed 3s videos of moving faces or moving objects as described in (35). Stimuli were presented in 18s blocks of 6 videos that subjects passively viewed. In six subjects, additional blocks of bodies, scenes and scrambled scenes were presented, but not analyzed for this study. Stimuli were presented in two runs, each of which contained four blocks per condition presented in palindromic order. Each run also contained two 18s fixation blocks at the start middle and end for a total run time of 180 s.

Subjects performed a theory of mind (ToM) task, as described in (36) and available http://saxelab.mit.edu/superloc.php. Participants read brief stories describing beliefs (ToM condition) or physical descriptions (control condition) and answered a true/false question about each story. Stories were presented for 10s followed by a 4s question period, and 12s fixation period at the beginning of end of each run for a total run time of 272 s. Stories were presented in two counter-balanced palindromic runs.

Data acquisition

Data were collected at the Athinoula A. Martinos Imaging Center at MIT on a Siemens 3T MAGNETOM Tim Trio Scanner with a 32-channel head coil. A high resolution T1-weighted anatomical image (multi-echo MPRAGE) was collected at each scan (repetition time [TR] = 2530 ms; echo time [TE] = 1.64 ms, 3.44 ms, 5.24 ms, 7.014 ms (combined with a RMS combination), echo spacing = 9.3 ms, bandwidth = 649 Hz/pixel, timing interval [TI] = 1400 ms, flip angle = 7, field of view [FOV] = 220x220 mm, matrix size = 220x220 mm, slice thickness = 1mm, 176 near-axial slices, acceleration factor = 3, 32 reference lines). Functional data were collected using a T2*-weighted echo planar imaging EPI pulse sequence sensitive to blood oxygen level dependent (BOLD) contrast (TR = 2000 ms, TE = 30 ms, echo spacing = 0.5 ms, bandwidth = 2298 Hz/pixel, flip angle = 90, FOV = 192x192 mm, matrix = 64x64 mm, slice thickness = 3 mm isotropic, slice gap = 0.3 mm, 32 near-axial slices).

Data preprocessing and modeling

Data preprocessing and general linear modeling was performed using Freesurfer Software Suite (freesurfer.net). All other analyses were conducted in Matlab (Mathworks). Preprocessing consisted of motion correcting each functional run, aligning it to each subjects’ anatomical volume and then re-sampling to each subject’s high-density surface computed by Freesurfer. After alignment, data were smoothed using a 5mm FWHM Gaussian kernel. For group-level analyses, data were co-registered to standard anatomical coordinates (Freesurfer

FSAverage template). All individual analyses were performed in each subject's native surface. General linear models included: one regressor per stimulus condition, as well as nuisance regressors for linear drift removal and motion correction (x,y,z) per run.

Group analysis

To test whether a systematic region across subjects that responded more strongly to social interactions than independent actions in Experiment 1, we ran a surface-based random effects group analysis across all subjects (holding out a single run) using Freesurfer. We first transformed the contrast difference maps for each subject to a common space (the Freesurfer fsaverage template surface). The group random effects analysis yielded an activation peak in right posterior STS. In subsequent analyses, we used the contiguous significant voxels ($p<10^{-4}$) around this peak as a group map to spatially constrain individual subjects' fROIs (described next).

ROI definition

To examine the region in the pSTS showing a selective response to social interactions in each subject, and to compare it to nearby fROIs that have previously been implicated in processing dynamic and/or social stimuli, we defined four regions of interest in each subject: right pSTS interaction region, pSTS face region, TPJ, and MT. Since the group random effects analysis only found significant selective responses to social interactions in the right hemisphere, we restricted our ROI analysis to the right hemisphere.

To define regions of interest in individual subjects, we used a group-constrained subject-specific approach (29, 51), where a functional or (in the case of MT) anatomical parcel was used to constrain individual subject's fROIs. For each subject, we defined each fROI as the top 10% most significant voxels for the relevant contrast (holding out one run of data) within the relevant parcel.

The group-based parcel used to spatially constrain the selection of the social interaction fROI was defined as the set of all voxels significant at the $p<10^{-4}$ level (uncorrected) in the group random effects contrast of social interaction> independent actions, that were contiguous and included the peak voxel.
In the same three out of four runs used to define the group map, we selected the top 10% of voxels in each subject, as that subject's social interaction fROI ("SI-fROI").

To define the pSTS face region, we use a parcel from (29) and identified the top 10% of most significant voxels showing a greater response to faces than object in one run of each subject's face localizer. To define the TPJ, we use the group map from (37), and selected the top 10% of significant voxels representing false belief>false physical task from one run of the theory of mind task. For the theory of mind task, we jointly model each story and question as a single event. Finally,

to define MT we use the Freesurfer anatomical MT parcel and the top 10% of significant voxels from all shape videos>task periods in Experiment 2.

To examine each region's response to the social interaction, face, and theory of mind contrasts, we measured the magnitude of response to each condition in each ROI in the held-out run. Because MT was defined in a hypothesis neutral manner (using all conditions), we did not hold out any data when defining the fROI.

Overlap analysis

To assess to the extent to which our three pSTS ROIs overlap with each other, we calculated the overlap between each pair of fROIs with respect to each of the two ROIs: size(A,B)/size(A) and size(A,B)/size(B), representing the proportion of one region that is overlapping with the other (34)To examine to what extent these regions represent distinct information, we excluded overlapping voxels from subsequent analyses.

MVPA

To test whether pattern information in our ROIs could distinguish helping versus hindering, we used the beta values from each ROI for the second 6s (the time period when the helping/hindering occurs) of each of the 10 help and 10 hinder videos. We trained a linear SVM (implemented with Matlab) to perform the binary classification between help and hinder videos. We trained the classifier on nine out of 10 help/hinder video pairs (leaving out one matched pair of help/hinder videos). We assessed the accuracy of the classifier by testing it on held out help/hinder pair of videos. We cycled through 10 hold out repetitions, and average the accuracy for each subject and ROI across these 10 runs. For each ROI we tested whether the average classification accuracy for all subjects was significantly above chance by comparing it with a chance classification of 0.5 (one-tailed t-test).

Amazon Mechanical Turk Ratings

To assess the saliency of the animacy, goals, and social interactions in the first 6s of each shape video, we collected ratings from 20 independent raters for each video on Amazon Mechanical Turk. Raters first watched a video of a screen capture from one continuous run of the shape experiment (Experiment 2) to familiarize them with the videos and task performed by subjects in the scanner. They then viewed the first 6s of each clip from the unseen run, and provided ratings (from 1=least to 4=most) for the animacy, goals, and social interactions of the shapes in each clip. We repeated this for both runs of the shape experiment to obtain 20 independent ratings for each video.

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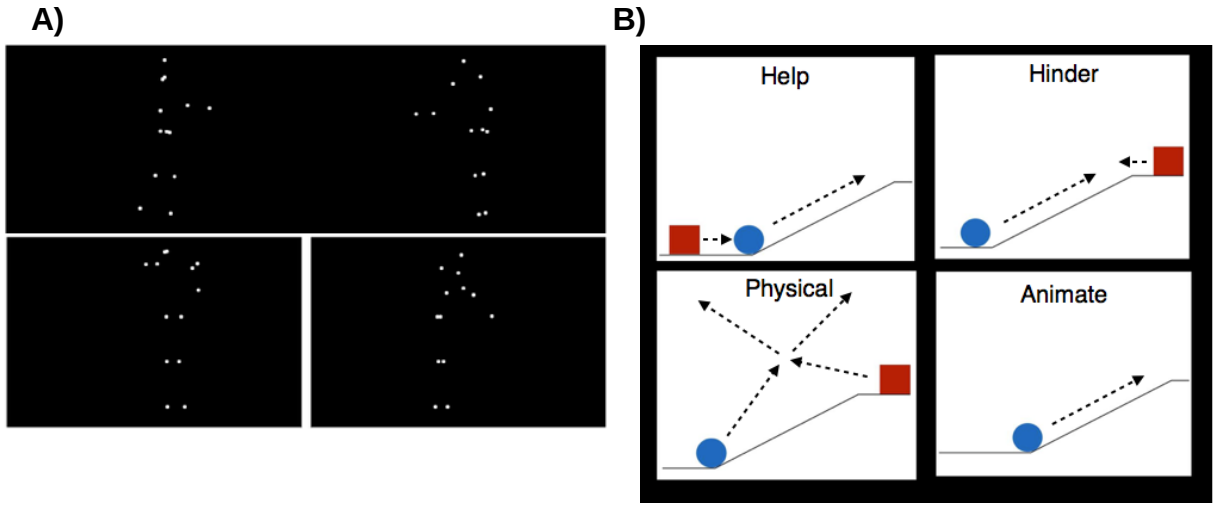


Figure 1 – Experimental stimuli. **A)** In Experiment 1, subjects viewed videos of two point-light figures either engaged in a social interaction (top), or conducting two independent actions with a white line drawn between the two actors to increase the impression that they were acting independently (bottom). **B)** In Experiment 2, subjects viewed videos of two animate shapes engaged in either a helping or hindering interaction (top). The first shape (in this example, blue) had a goal (e.g. climb a hill) and the second shape either helped (top, left) or hindered (top, right) the first shape. We contrasted these two interaction conditions with two further conditions: a "physical" interaction condition in which the two shapes moved in an inanimate fashion like billiard balls (bottom, left), and an "animate" condition containing a single goal-oriented, animate shape (bottom, right). See Supplemental Videos 1-4 for an example of each of the four types of shape videos.

A) **B)**

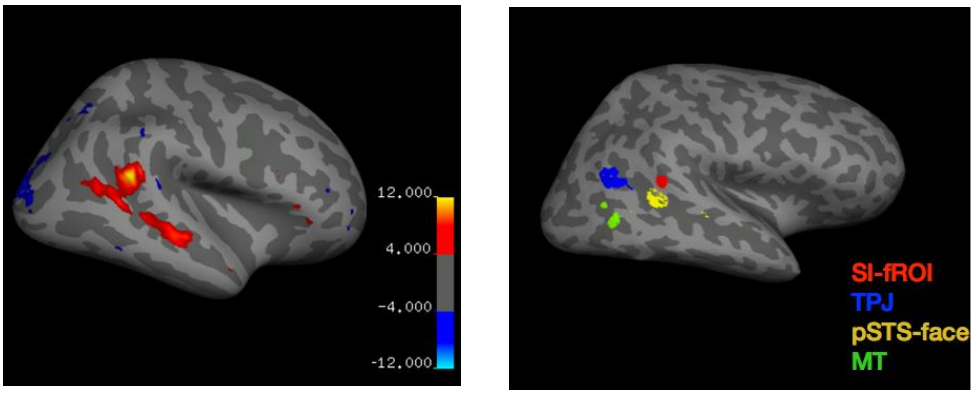


Figure 2 – Selectivity to social interactions in the posterior STS. **A)** A group random effects map for the interaction versus independent point-light walker contrast in Experiment 1 showing a peak of activity in the right pSTS, with weaker activity along the STS. Color bar indicates negative log of the p level for the interaction > independent contrast in that voxel. B) The locations of the individually defined fROIs for one subject, including the social interaction fROI (SI-fROI) in red, the TPJ in blue, the pSTS-face region in yellow, and MT in green. Individual-subject fROIs were defined with a group-constrained subject-specific analysis (see Methods) and showed a consistent spatial organization across subjects, with the SI-fROI falling anterior to the TPJ and superior to the pSTS-face region.

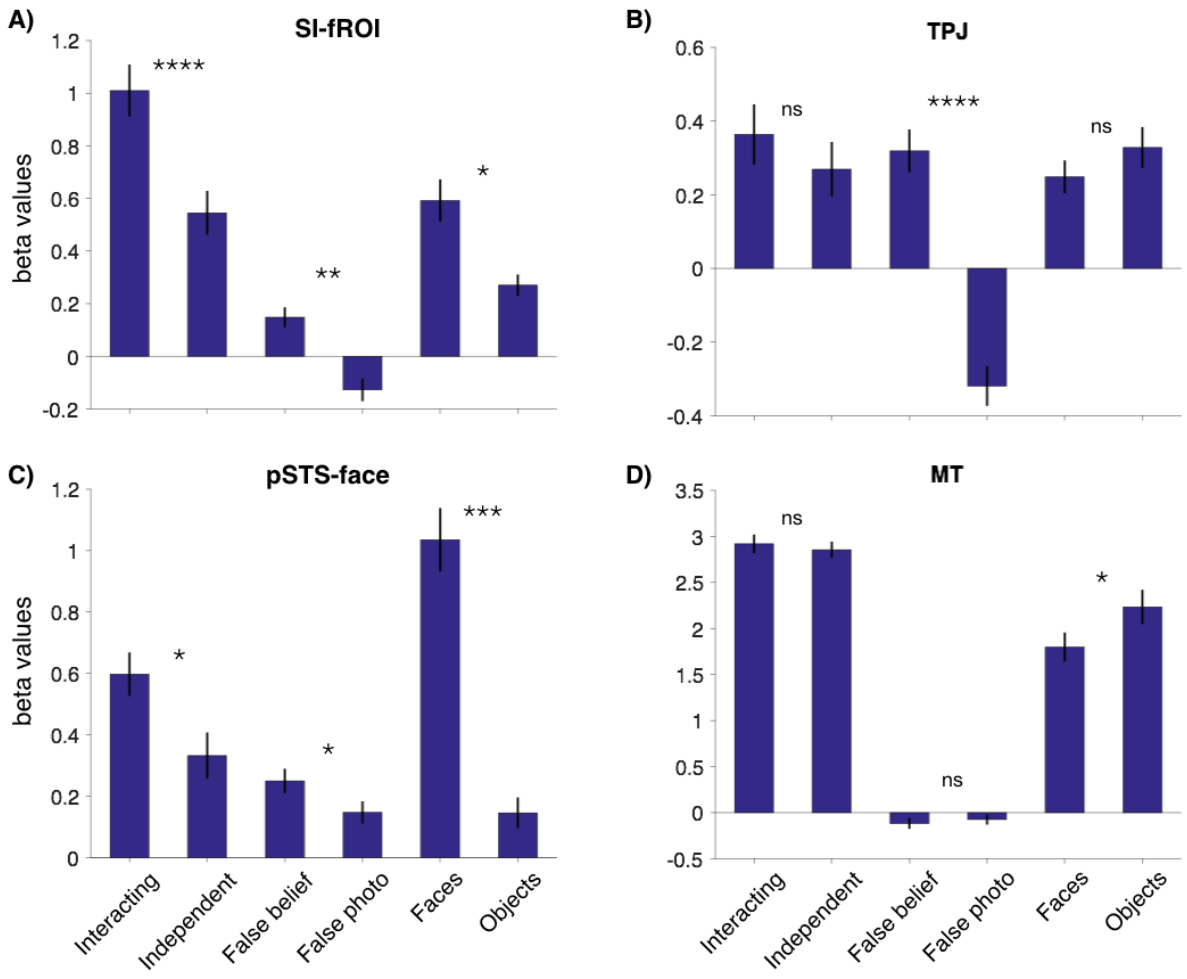


Figure 3 – fROI responses to Experiment 1 stimuli. The average beta values (mean +/- SEM) across subjects in each individually-defined fROI to each condition from the three fROI-defining contrasts: point light walkers interacting vs. independent (Experiment 1), false belief vs. false photo stories (standard TOM localizer), and faces vs. objects. The beta values are all calculated from a held-out localizer run that was not used to the define the fROI. Significance is denoted with asterisks (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001, ****p ≤ 0.0001).

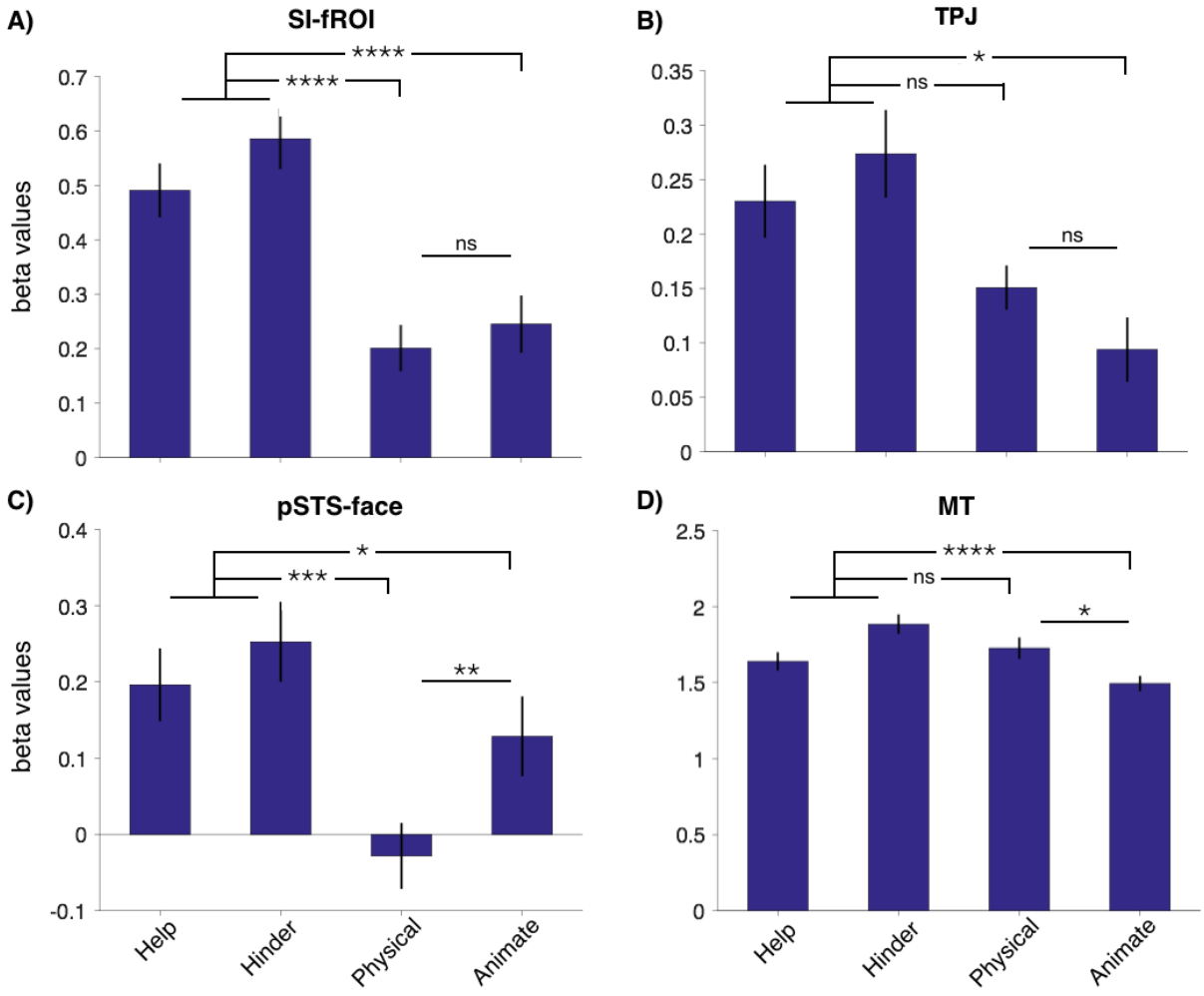


Figure 4 – fROI responses to Experiment 2 shape stimuli. The average beta values (mean +/- SEM) across subjects in each individually-defined fROI to the first six seconds of the help, hinder, physical interaction, and animate videos. Significance is denoted with asterisks (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001, ****p ≤ 0.0001).

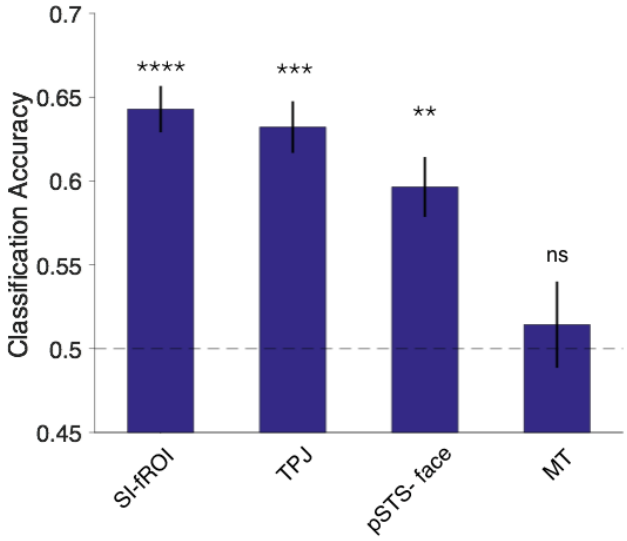
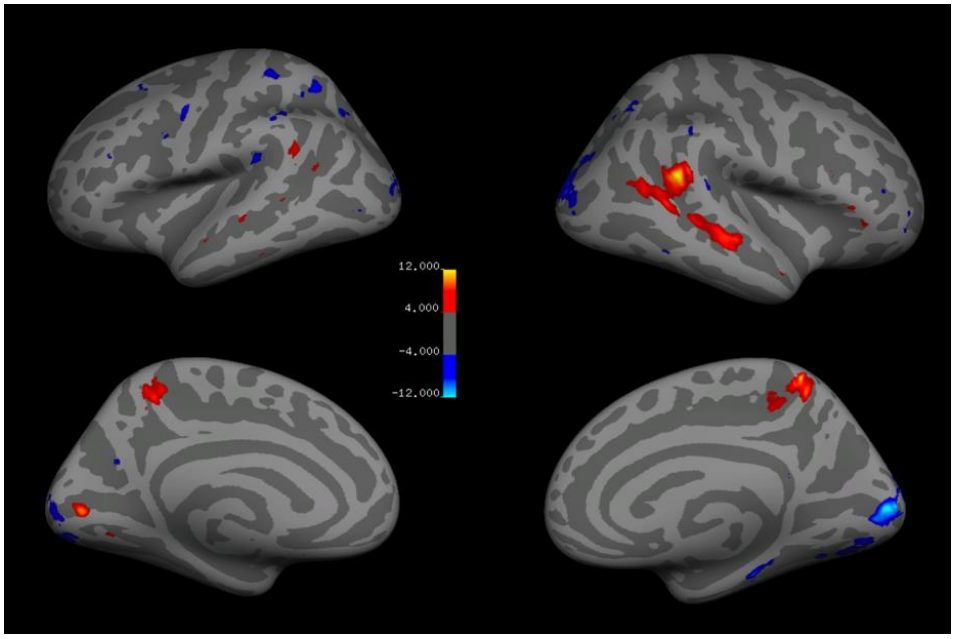


Figure 5 – Decoding helping versus hindering conditions. Average classifier accuracy (mean +/- SEM) across subjects in each fROI for decoding help versus hinder. A linear SVM classifier was trained on the beta values from nine pairs of videos in each individual subjects' fROIs and tested on the tenth held-out pair. Significance is denoted with asterisks (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001, ****p ≤ 0.0001).

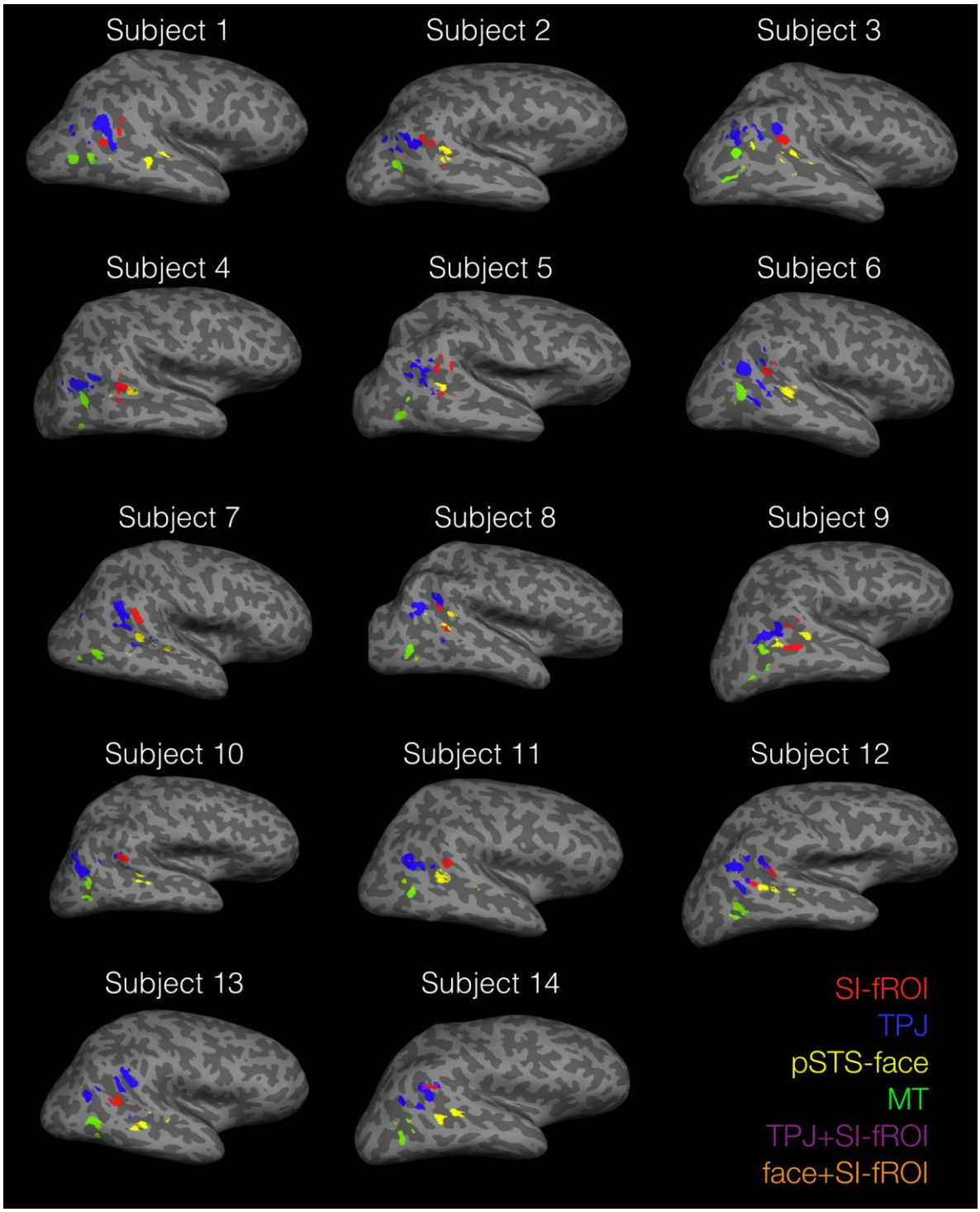
Supplemental Materials

Subject	SI-fROI and TPJ (% of SI-fROI)	SI-fROI and pSTS-face (% of SI-fROI)	SI-fROI and TPJ (% of TPJ)	SI-fROI and pSTS-face (% of pSTS-face)
1	0.00	0.00	0.00	0.00
2	0.01	0.00	0.00	0.00
3	0.06	0.00	0.02	0.00
4	0.04	0.06	0.01	0.06
5	0.05	0.00	0.02	0.00
6	0.00	0.00	0.00	0.00
7	0.00	0.02	0.00	0.02
8	0.13	0.08	0.03	0.08
9	0.00	0.01	0.00	0.01
10	0.05	0.00	0.01	0.00
11	0.00	0.00	0.00	0.00
12	0.25	0.00	0.06	0.00
13	0.01	0.00	0.00	0.00
14	0.59	0.00	0.17	0.00
Average	**0.08**	**0.01**	**0.02**	**0.01**

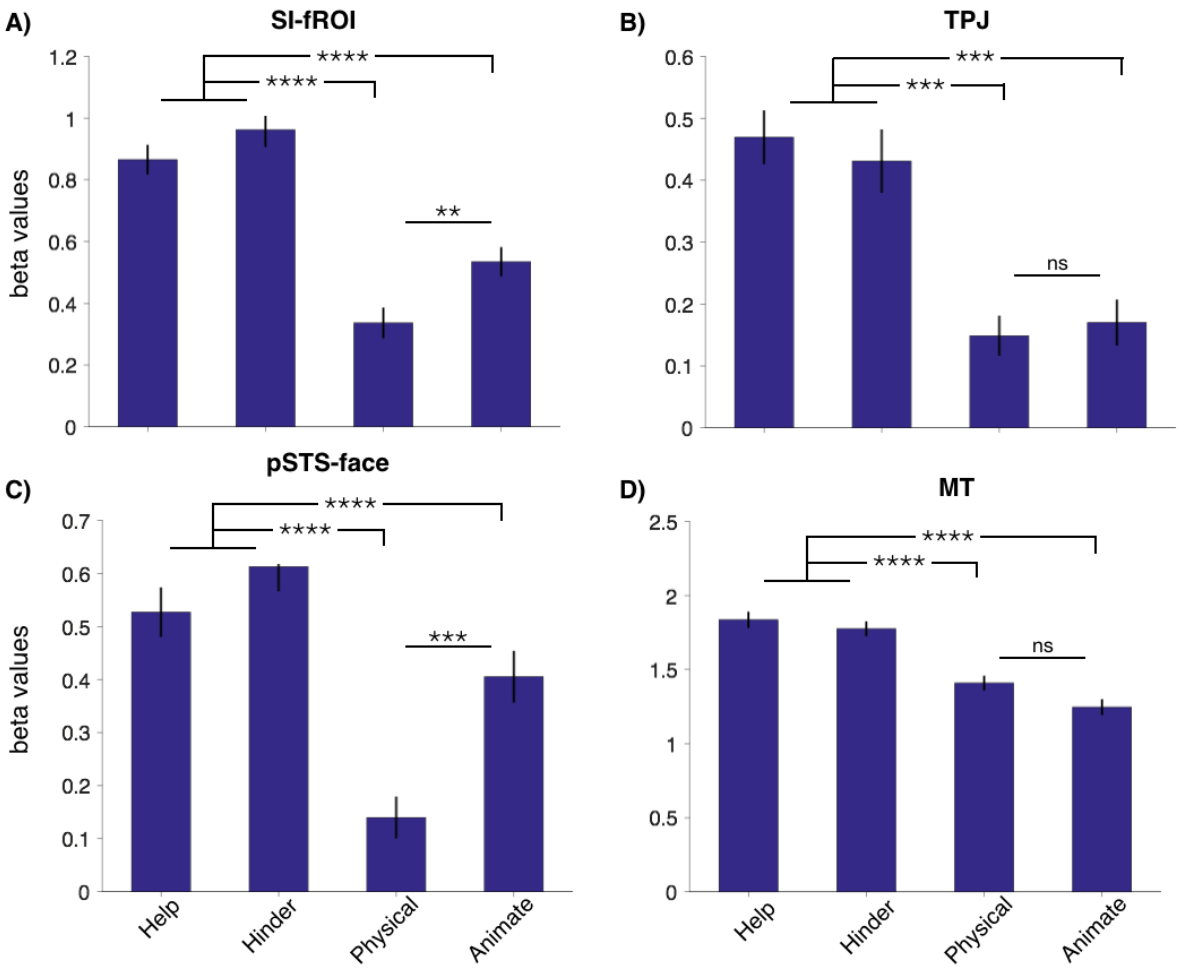
Supplemental Table 1 – fROI overlap. The overlap between each individual subject's SI-fROI and the TPJ, and the SI-fROI and the pSTS-face region. Overlap is calculated in two ways, first as a percentage of voxels of the SI-fROI (the number of overlapping voxels divided by the number of voxels of the SI-fROI, columns 2-3), and second as a percentage of voxels of the second fROI (the number of overlapping voxels divided by the number of voxels in the TPJ or pSTS-face, columns 4-5, respectively).



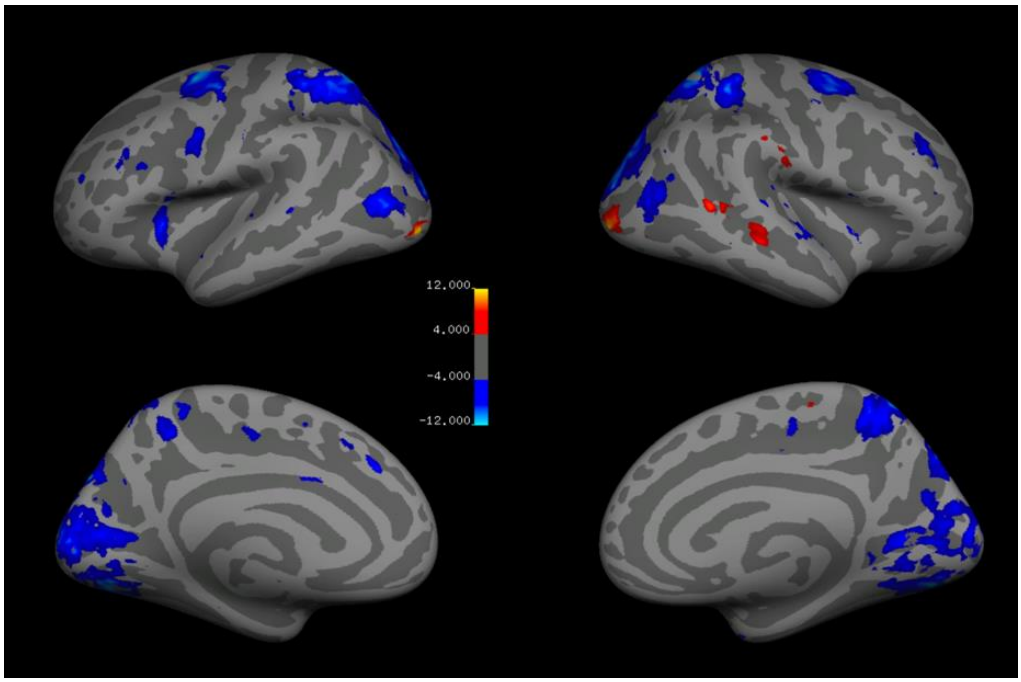
Supplemental Figure 1 – Group random effects analysis (n = 14) for Experiment 1 (social interaction > independent), shown for lateral and medial views of the left and right hemispheres. (MNI coordinate of peak activation = [53.95, -43.17, 17.56].)



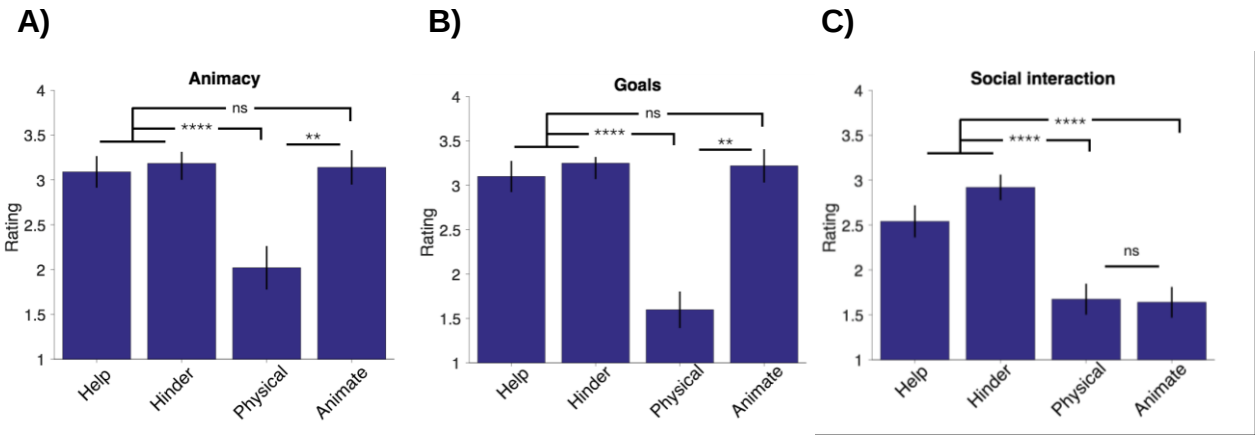
Supplemental Figure 2 – fROI locations in individual subjects, defined with the top 10% of most significant voxels for each localizer contrast in the group-constrained subject-specific analysis (see Methods).



Supplemental Figure 3 – fROI responses to the four stimulus conditions in Experiment 2. The average beta values (mean +/- SEM) across subjects in each individually-defined fROI to the second six seconds of the help, hinder, physical interaction, and animate videos. Significance is denoted with asterisks (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001, ****p ≤ 0.0001).



Supplemental Figure 4 – A whole brain group random effects analysis (n = 12) for the first six seconds of the animate versus physical interaction shape videos (Experiment 2). As previously reported, there is increased activity for animate > physical interactions in right STS, inferior to the peak observed in the group RFX for social interaction > independent (Figure 1A).



Supplemental Figure 5 – Average ratings (from 1, least to 4, most) for the A) animacy and B) saliency of goals, and C) social interactions for the first 6s of each of the shape video conditions, averaged over 20 ratings from separate Amazon Mechanical Turk videos for each of the 10 videos (error bars represent mean +/- SEM across raters). Significance is denoted with asterisks (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001, ****p ≤ 0.0001).

Supplemental Videos 1-4
Four example videos from Experiment 2, for the (1) help, (2) hinder, (3) physical, and (4) animate conditions.

Supplemental Video 1:
http://web.mit.edu/bcs/nklab/KanSocStims/02_help.m4v.avi

Supplemental Video 2:
http://web.mit.edu/bcs/nklab/KanSocStims/02_hinder.m4v.avi

Supplemental Video 3:
http://web.mit.edu/bcs/nklab/KanSocStims/02_physics.m4v.avi

Supplemental Video 4:
http://web.mit.edu/bcs/nklab/KanSocStims/02_animate.m4v.avi

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